REVISION OF *LOBELIA* SECT. *TUPA* (CAMPANULACEAE: LOBELIOIDEAE)

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ABSTRACT

The classification of *Lobelia* L. sect. *Tupa* (G. Don) Benth. was revised following extensive field studies and examination of over 2500 specimens in 43 herbaria. Four species are recognized; all are hexaploids with racemose unilabiate flowers, endemic to central Chile. Two are branched solid-stemmed shrubs (rarely small trees) with faintly striate oblong or ellipsoid seeds, found in the dwarf- and xerophytic-shrub and sclerophyllous vegetation zones of the xeric north: *L. polyphylla* Hook. & Arn. with small wine-purple flowers, and *L. excelsa* Bonpl. with larger flowers that change color from yellow and orange in bud to red at anthesis. The other two are large herbaceous or suffruticose unbranched hollow-stemmed perennials with minutely foveolate-reticulate broadly ellipsoid seeds, found in the deciduous forest and evergreen temperate rain forest regions of the mesic south: red-flowered *L. tupa* L. and pink-flowered *L. bridgesii* Hook. & Arn. The species of each pair are at least partly sympatric, and their reproductive isolation (as evidenced by a near total lack of plants with intermediate morphology) may be related to differences in pollination syndrome: entomophily in *L. bridgesii* and *L. polyphylla*, ornithophily in *L. tupa* and *L. excelsa*.

RESUMEN

La clasificación de *Lobelia* L. sect. *Tupa* (G. Don) Benth. se revisó como continuación a estudios de campo extensivos y el examen de más de 2500 especímenes de 43 herbarios. Se reconocen cuatro especies, todas ellas hexaploides con flores unilabiadas racemosas, endémicas de Chile central. Dos son arbustos ramosos de tallos sólidos (raramente pequeños árboles) con semillas oblongas o elipsoides débilmente estriadas, que se encuentran en las zonas de vegetación de arbustos enanos xerofíticos y la zona esclerófila del norte xérico: *L. polyphylla* Hook. & Arn. con flores pequeñas de color púrpura-vino, y *L. excelsa* Bonpl. con flores más grandes que cambian de color desde el amarillo y naranja en el botón, hasta rojo en la antesis. Las otras dos son perennes herbáceas grandes o sufruticosas no ramosas de tallo hueco, con semillas anchamente elipsoides diminutamente foveolado-reticuladas, que se encuentran en las regiones de la pluvisilva caducifolia y la templada perennifolia del sur mésico: *L. tupa* L. de flores rojas y *L. bridgesii* Hook. & Arn. de flores rosas. Las especies de cada par son al menos parcialmente simpátricas, y su aislamiento reproductivo (como se evidencia por la falta casi total de plantas con morfología intermedia) puede estar relacionado con diferencias en el síndrome de polinización: entomofilia en *L. bridgesii* y *L. polyphylla*, y ornitofilia en *L. tupa* y *L. excelsa*.

Lobelia L. is the largest genus of Lobelioideae (Campanulaceae), comprising over 400 species of annual and perennial herbs, shrubs, trees, and giant rosette plants (Lammers 1993a). It is cosmopolitan in distribution, indigenous to six continents and several island groups (e.g., Hawaii, New Zealand, the Antilles). Nearly 38% of the species are African and another 29% North American; Asia and Australasia each have about 10% of the species, South America 8%, and Polynesia 3%, while only two species occur in Europe (Lammers, unpublished data).

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The genus was last monographed by Wimmer (1953, 1968), who divided it into three subgenera: *Lobelia* with two sections; *Mezleria* (C. Presl) E. Wimm., nom. illeg. (cf. Lammers 1999) with two sections; and *Tupa* (G. Don) E. Wimm. with six sections. Further taxonomic structure was indicated by dividing many of the sections into subsections and other subordinate taxa (cf. Lammers 1993a).

Wimmer's classification of *Lobelia* was recently revised by Murata (1995). Though based primarily on seed coat morphology (Murata 1992), this revision was also concordant with other data not available to Wimmer, including chromosome numbers (Lammers 1993a) and chloroplast DNA (cpDNA) restriction-site analyses (Knox et al. 1993). In this classification, Wimmer's three subgenera were maintained (though the illegitimate name of the second one should be replaced by subg. *Isolobus* (A. DC.) Y.S. Lian; Lammers 1999). However, Wimmer's division of the subgenera into sections was greatly altered.

Among the sections of subg. *Tupa* which were remodeled by Murata was sect. *Tupa* (G. Don) Benth. Wimmer (who used the now illegitimate name sect. *Eutupa* E. Wimm.) had construed this section to include 69 diverse species from Asia, Africa, South America, and the West Indies. (Within the section, however, Wimmer did segregate the Chilean species as "§1. Species chilenses" under the invalid subsectional name "Primanae", nom. nud.) In Murata's revision, however, all extra-Chilean species were removed to sect. *Colensoa* (Hook. f.) J. Murata or sect. *Homochilus* A. DC., leaving only a small group of species endemic to central Chile in sect. *Tupa*.

Thus circumscribed, sect. *Tupa* is characterized by its combination of robust iteroparous (polycarpic) habit; large racemose flowers; unilabiate red, pink, or wine-purple non-spurred corolla with monomorphic deflexed lobes coherent at apex; staminal column shorter than the corolla and exserted from its dorsal slit; ventral anthers bearded apically with tufts of stiff white trichomes; smooth seed coat comprising a single layer of cells with long lumina (Type D of Murata 1992, 1995); and hexaploid ($n = 21$) chromosome number. The latter two features appear to be unique within subg. *Tupa* (Murata 1992, 1995; Knox et al. 1993; Lammers 1993a). While hexaploidy is regarded as derived within Lobelioideae (Lammers 1993a), the Type D seed coat is considered plesiomorphic (Murata 1992, 1995).

This more restricted circumscription was supported strongly by the phylogenetic analyses based on cpDNA data (Knox et al. 1993). In the concensus tree, the species of sect. *Tupa* s. str. formed a monophyletic group that was supported by 10 cpDNA restriction-site mutations (bootstrap value 99%, decay value >5). The remaining species of subg. *Tupa* examined, including two (*L. boninensis* Koidz. and *L. nicotianifolia* Roth ex Schult.) that had been included in sect. *Tupa* by Wimmer, formed its sister-group. These plants were all tetraploid ($n = 14$), so far as known (Lammers 1993a).

TAXONOMIC HISTORY

Plants referable to *Lobelia* sect. *Tupa* were first made known to Europeans through the activities of the French missionary Louis Feuillée, who visited Chile between 1707 and 1712. In the published account of his travels (Feuillée 1714), he described and illustrated

a highly toxic plant known to the indigenous Mapuche as *tupa*. Feuillée gave the plant the Latin polynomial "Rapuntium spicatum, foliis acutis, vulgò Tupa." In *Species plantarum*, Linnaeus (1753) accepted the species on the sole basis of Feuillée's description and plate, and assigned it to his genus *Lobelia*. In taking up the vernacular name as the *nomen triviale*, he misspelled it "trapa." This error was corrected to *L. tupa* in the next edition (Linnaeus 1762).

In the first half of the nineteenth century, 17 species related to *L. tupa* were described from Chile. More than one-third of these descriptions (e.g., Sims 1810; Lindley 1826, 1830; D. Don 1835) were based on plants cultivated from seed in various European botanic gardens, and were published in illustrated semi-popular venues such as *Curtis's Botanical Magazine*. In the latter half of the century, eight more species were described, primarily by resident botanist Rodulfo Amando Philippi (1808–1904) in the course of his studies of the Chilean flora (e.g., Philippi 1873, 1895). A number of varieties and forms were also described over the years by various workers. Altogether, 35 heterotypic taxa referable to *Lobelia* sect. *Tupa* have been described, all from Chile and nearly all in the nineteenth century.

Differences of opinion on the circumscription and typification of genera created additional combinations in the group. Presl (1836) believed that *Rapuntium* Mill. was the nomenclaturally correct name for most of the species treated under *Lobelia* by Linnaeus, while Kuntze (1891) argued for *Dortmanna* Hill. George Don (1834) segregated robust species of *Lobelia* with unilabiate corollas as the genus *Tupa* G. Don, a move supported by Candolle (1839) but subsequently reversed by Bentham (1876). These differences of opinion (together with changes in rank by various workers over the years) have resulted in an additional 61 homotypic combinations based on the original 35 taxa, giving a total of 96 validly published names referable to *Lobelia* sect. *Tupa*.

In the most recent flora of Chile, Reiche (1905, 1910) synonymized or excluded many of these names, recognizing just six species and six additional heterotypic varieties in sect. *Tupa*. In the most recent monograph of the section (as "§1. Species chilenses"), Wimmer (1953, 1968) recognized 20 taxa: seven species plus thirteen additional heterotypic varieties and forms. This classification was implicitly accepted by Murata (1995) when he remodeled the section, and was also embodied in the most recent catalogue of the Chilean flora (Marticorena & Quezada 1985). However, when I began to prepare a treatment of the Campanulaceae for *Flora de Chile* (cf. Marticorena & Rodríguez 1995), it became apparent that this classification of the section was less than optimal, and that a thorough revision was required.

ETHNOBOTANY

Though *tupa* (sometimes rendered as *trupa*) is the Araucanian name for *L. tupa*, the plant is also widely known in Spanish as *tabaco del diablo* (Santa Cruz 1932; Ibáñez 1955; Mariani 1965; Hoffmann 1997). This common name ("devil's tobacco") relates to early reports that the dried leaves were smoked by the Mapuche for "unholy" purposes, i.e., as a narcotic and alleged hallucinogen. Although its hallucinogenic status has not been dem-

onstrated clinically, the plant was considered by Schultes (1981, 1990) to be "definitely psychoactive." The actual compounds responsible for this activity are not known. The latex does contain pyridine alkaloids, including lobeline and its diketo- and dihydroxy-derivatives, lobelanidine and nor-lobelanidine (Santa Cruz 1932; Hill 1970; Raffauf 1970; Gibbs 1974); however, these substances are not pyschoactive (Schultes & Hoffmann 1980). Lobeline has been used pharmaceutically as a respiratory stimulant, in the treatment of bronchial asthma symptoms, and in overcoming nicotine addiction (Blacow 1972; Lewis & Elvin-Lewis 1977). In Chile, the expressed latex of *L. tupa* has been used by rural folk to relieve the pain of dental caries, and in compresses to treat joint and hoof pain in horses (Murillo 1889; Santa Cruz 1932). The pharmacological bases for such uses are not known.

Hallucinogenic or not, *L. tupa* is definitely toxic. Feuillée (1714) reported that the odor of the flowers alone was enough to induce vomiting. Despite several trials, I was not able to confirm that observation, though the scent is by no means pleasant. In any event, beekeepers consider the plant a nuisance, as its nectar gives honey an acrid, unpleasant flavor (Murillo 1889). Though ostensibly a hummingbird-pollinated plant (see below), I have observed large orange bees stealing nectar from the flowers via the dorsal slit of the corolla, without contacting the anthers or stigma.

Feuillée also reported that small quantities of latex rubbed in the eyes would cause blindness, a statement I can partly confirm. On more than one occasion during field work, I absent-mindedly rubbed my eye after handling material of *L. tupa*. Though latex was no longer perceptible on my hands, in a short time my eye began to sting and water profusely and my vision blurred, while the surrounding skin of the face became swollen and numb. The effects persisted for nearly an hour. Murillo (1889) reported that ingestion of the plant or its latex could result in intestinal distress and bloody diarrhea. Most recently, Matthews (1988) documented the case of a London gardener who was immobilized for 10–15 minutes after accidentally inhaling airborne dried latex of the plant.

On a more pleasant note, the species of *Lobelia* sect. *Tupa* have considerable horticultural potential. When seed was first imported to Europe early in the nineteenth century, the resulting plants generated a great deal of interest among gardeners and plant aficionados (Sims 1825; Lindley 1826, 1830, 1833; G. Don 1834; D. Don 1834, 1835; Lemaire 1843; Loudon 1844). Though most were soon lost from cultivation, *L. tupa* apparently remained in the trade (Voss 1894; Finnis 1966; Matthews 1988; Thomas 1990; Huxley 1992) and may have been the object of some selective breeding; Chittenden (1923) mentions a cultivar from Stokes' nursery named 'Brilliant.' However, seed of the three other species recognized here has been reintroduced to botanic gardens (Lammers 1993b), which may lead to a renewal of interest in these plants as horticultural subjects.

SYSTEMATICS

Much of the data upon which this revision is based was gathered from over 2500 specimens deposited in 43 herbaria (see Acknowledgments for a complete list of institutions). This was supplemented by 10 weeks of intensive field work in Chile during January 1989 and October–November 1990. In company with one to three Chilean colleagues, I

travelled over 6500 miles by jeep, covering the entire geographic, elevational, and ecological range of sect. *Tupa*, from Copiapó (27°20'S) in the north to Puerto Montt (41°30'S) in the south. Fifty-six natural populations, representing all species recognized here, were visited and studied. I was also able to examine several naturalized populations of *L. tupa* in the Juan Fernández Islands during an expedition in January-February 1986 (cf. Lammers 1997).

During these studies, particular attention was paid to patterns of morphological variation within populations. Though some of the infraspecific taxa recognized by Wimmer (1953, 1968) are quite striking, if they do not at a minimum form discrete populations, they do not merit taxonomic recognition. Emphasis was also placed on discerning possible geographic, elevational, or ecological correlates of morphological variation. In addition, material was also gathered for cytological investigations. The results of that work were reported separately (Lammers & Hensold 1992).

In the end, it was concluded that only four species and no infraspecific taxa could be distinguished in sect. *Tupa: L. bridgesii* Hook. & Arn. [including *L. blanda* (D. Don) Endl.], *L. excelsa*, *L. polyphylla* [including *L. ovata* Reiche], and *L. tupa* [including *L. mucronata* Cav.]. The rationale for each of these synonymizations is discussed under the respective species.

These four species can be divided readily into two pairs on the basis of habit, seed morphology, and habitat: (1) a pair of branched solid-stemmed shrubs (rarely small trees) with faintly striate oblong or ellipsoid seeds, in the dwarf- and xerophytic-shrub and sclerophyllous vegetation zones of the xeric northern portion of the range (*L. excelsa* and *L. polyphylla*); and (2) a pair of robust herbaceous or suffruticose unbranched hollow-stemmed perennials with minutely foveate-reticulate broadly ellipsoid seeds, in the deciduous forest and evergreen temperate rain forest regions of the mesic southern portion (*L. bridgesii* and *L. tupa*).

The two pairs are largely allopatric, though populations of *L. excelsa* and *L. tupa* do approach within a few miles of each other in Prov. Colchagua, Curicó, and Talca. The members of each pair are definitely sympatric. In the xeric north, the geographic ranges of *L. excelsa* and *L. polyphylla* overlap by roughly 90%; the former extends a little farther south and not so far north, while the latter generally grows nearer the sea and not so high into the Andean foothills. In the mesic south, *L. bridgesii* has a very restricted distribution that lies entirely within the broader range of *L. tupa*.

Not only are the members of each pair sympatric, they often form mixed populations. Of the 17 populations studied in the mesic south, 76% comprised *L. tupa* only, 18% *L. bridgesii* only, and 6% were mixed. Of the 39 populations studied in the xeric north, 54% comprised *L. excelsa* only, 26% *L. polyphylla* only, and 21% were mixed.

Despite this apparent opportunity for miscegenation, I could not locate a single morphologically intermediate individual during field work, despite intensive searches. Furthermore, I have examined only one herbarium specimen that clearly is intermediate between two accepted species. The holotype of *Tupa kingii* Phil., collected at Valparaíso in 1868, appears to represent *L. excelsa* × *L. polyphylla* (see below).

From these facts, it is apparent that some very efficient isolating mechanism is at work among these species. Differences in chromosome number may be ruled out; all

have $n = 21$, interpreted as hexaploid (Lammers & Hensold 1992; Lammers 1993a; but cf. Stace & James 1996 for an alternative interpretation). Phenological differences likewise do not appear to be operative. Though *L. polyphylla* begins to bloom a few weeks earlier than *L. excelsa,* there is still very considerable overlap in their respective phenologies; *L. bridgesii* and *L. tupa* bloom concurrently.

The best hypothesis is that isolation within each pair is a product of pollinator differences, a situation similar to that hypothesized for *L. cardinalis* L. and *L. siphilitica* L. (Thompson & Lammers 1997). Judging from floral morphology, it appears that one member of each pair is adapted to entomophily, the other to ornithophily. The flowers of *L. bridgesii* and *L. polyphylla* appear suitable for effective visits by bees and other insects. I have not observed pollinator visits to *L. polyphylla,* but large orange bees were observed visiting flowers of *L. bridgesii,* contacting the anthers and stigmas with their backs. When the same bees visited *L. tupa,* it was as a nectar thief, removing nectar via the dorsal slit without touching anthers or stigma. With their larger red flowers, *L. excelsa* and *L. tupa* appear to be adapted to pollination by hummingbirds, though I have not observed this. Further biosystematic research clearly is needed to test these hypotheses.

While the four species fall into two pairs on the basis of habit, seed morphology, and habitat, this does not appear to be an accurate reflection of the underlying phylogeny, as inferred from cpDNA restriction-site mutations (Knox et al. 1993). Though the southern pair (*L. bridgesii* and *L. tupa*) is supported as a clade by three shared mutations (bootstrap value 95%, decay index = 3), the northern pair is not. Instead, *L. polyphylla* forms the basal branch of the tree, sister to the remaining three species; *L. excelsa* is then the next branch, sister to the southern pair. The sister-relationship of *L. excelsa* to the southern pair is likewise supported by three mutations (bootstrap value 93%, decay index = 3).

Though no detailed non-molecular analyses have been performed, it does appear that morphological data are concordant with the cpDNA phylogeny. *Lobelia polyphylla,* the basal branch, is the most discordant member of the section, with its much smaller wine-purple flowers. The members of the (*L. excelsa* + southern pair) clade all share larger red (or pink) flowers, while the southern pair is characterized by its unbranched hollow herbaceous or suffruticose stems, usually decurrent leaf margins, and minutely foveate-reticulate broadly ellipsoid seeds. Unique traits within the (*L. excelsa* + southern pair) clade are the pink corolla of *L. bridgesii;* and the tan or pale yellow latex, bibracteolate pedicels, and floral color change (Weiss 1995) of *L. excelsa.* Statements regarding the apomorphy or plesiomorphy of any of these traits are best deferred pending better knowledge of the outgroup.

Lobelia sect. **Tupa** (G. Don) Benth. in Benth. & Hook. f., Gen. Pl. 2:552. 1876. *Tupa* G. Don, Gen. Hist. 3:700. 1834. *Lobelia* [unranked] *Tupa* (G. Don) Heynh., Nom. Bot. Hort. 1:473. 1840. *Lobelia* sect. *Eutupa* E. Wimm., Ann. Naturhist. Mus. Wien 56:365. 1948, nom. illeg. TYPE (under Art. 22.5, first confirmed by Pfeiffer 1874): *L. tupa* L.

Iteroparous shrubs, 0.6–4 m tall (rarely small trees to 6.8 m tall) or robust perennials, 0.5–3 m tall; stems woody, solid, and repeatedly branched, or herbaceous or suffruticose,

hollow, and unbranched above the base, pubescent or glabrous; latex white, less often pale yellow or tan. Leaves simple, alternate, exstipulate, pinnately veined, sessile, pubescent or glabrous; margin entire or finely callose-toothed, sometimes forming a sagittate base decurrent on the stem below the point where the midrib meets the node. Flowers perfect, protandrous, resupinate, epigynous, zygomorphic, pedicellate, solitary in the axils of the upper leaves or these reduced in size, creating a terminal 10—65-flowered bracteate anauxotelic (rarely auxotelic) racemose inflorescence; pedicel equalling or shorter than its flower, ebracteolate or with a pair of linear bracteoles at or below the middle. Hypanthium obconic, hemispheric, campanulate, or obovoid, pubescent or glabrous, adnate to the ovary; calyx lobes 5, valvate, triangular or narrowly triangular, pubescent; margin entire or very rarely with a few teeth. Corolla sympetalous, unilabiate, 15–65 mm long, red (sometimes yellow and orange in bud, or very rarely all yellow throughout anthesis), pink, or wine-purple, lacking a nectar spur, glabrous or minutely pubescent; tube suberect, curved, or arcuate, slit dorsally to base; lobes 5, valvate, monomorphic, shorter than the tube, deflexed, coherent at apex. Stamens 5, alternating with the corolla lobes, connate, forming a staminal column shorter than the corolla and free from it; filament tube exserted through dorsal slit in corolla, bearing small flattened triangular trichomes ventrally at base, otherwise glabrous; anthers dehiscing introrsely and longitudinally, the dorsal three longer than the ventral two, occluding the orifice of the tube, the surface of the tube glabrous or the dorsal three with scattered long hairs, the ventral two with tufts of white bristles at apex. Ovary inferior, bilocular; placentae axile, large; ovules numerous, small, anatropous. Fruit a half-inferior capsule, broadly ellipsoid, ovoid, obovoid, oblate, or subspherical, dehiscent by two valves at the rounded or truncate and apiculate apex. Seeds small, light brown or golden brown, oblong or ellipsoid and faintly striate, or broadly ellipsoid and minutely foveolate-reticulate; testa comprising a single layer of cells with long lumina (Type D of Murata 1992, 1995). Chromosome number $n = 21$. Four species, endemic to central Chile.

KEY TO THE SPECIES

1. Shrubs (rarely small trees); stems woody, repeatedly branched, solid; leaf base not lobed, not decurrent on stem; seeds oblong or narrowly ellipsoid, the surface faintly striate.
   2. Latex white; pedicels ebracteolate or very rarely with a pair of bracteoles 2–5 mm long; hypanthium 4–8 mm in diameter; corolla 15–25 mm long, wine-purple, the tube (7–)10–17 mm long, the lobes 4–12 mm long; filament tube 9–15 mm long; anther tube 4–7 mm long, glabrous or very rarely sparsely pubescent; capsule 6–9 mm in diameter _____ **1. L. polyphylla**
   2. Latex tan or pale yellow; pedicels with a pair of bracteoles 2.5–10 mm long; hypanthium 8–15 mm in diameter; corolla (38–)45–65 mm long, yellow and orange in bud, becoming red at anthesis (very rarely all yellow throughout anthesis), the tube 25–42 mm long, the lobes 12–33 mm long; filament tube 29–47 mm long; anther tube 8–11 mm long, pubescent; capsule 11–18 mm in diameter _____ **2. L. excelsa**

1. Robust perennial herbs; stems herbaceous or suffruticose, unbranched above the base, hollow; leaf base sagittate, the pair of triangular basal lobes decurrent on the stem for 2–30 mm (rarely cuneate or obtuse and non-decurrent); seeds broadly ellipsoid, the surface minutely foveolate-reticulate.
   3. Leaf apex acute or acuminate, sometimes mucronate or cuspidate; lamina, hypanthium, and calyx lobes densely pubescent; corolla 31–49 mm long, red (very rarely yellow), densely pubescent, the tube 19–35 mm long; filament tube 22–33 mm long _____ **3. L. tupa**
   3. Leaf apex long acuminate, aristate or cirrhose; lamina, hypanthium, and calyx lobes glabrous; corolla 25–36 mm long, pink, glabrous, the tube 13–19 mm long; filament tube 14–17 mm long _____ **4. L. bridgesii**

1. Lobelia polyphylla Hook. & Arn., Bot. Beechey Voy. 33. Dec 1830. *Tupa polyphylla* (Hook. & Arn.) G. Don, Gen. Hist. 3:700. 1834. *Rapuntium polyphyllum* (Hook. & Arn.) C. Presl, Prodr. Monogr. Lobel. 29. 1836. *Dortmanna polyphylla* (Hook. & Arn.) Kuntze, Revis. Gen. Pl. 972. 1891. TYPE: CHILE. Valparaíso, [26 Oct–2 Nov 1825 *or* May 1828, leg. Lay & Collie,] *Beechey s.n.* (HOLOTYPE: K!). Information in brackets is taken from the official itinerary (Hooker & Arnott 1830).

Lobelia purpurea Lindl., Edwards' Bot. Reg. 16:pl. 1325. Jun 1830; non Breiter, Hort. Breiter. 249. 1817. *Tupa purpurea* G. Don, Gen. Hist. 3:700. 1834. *Rapuntium purpurea* (G. Don) C. Presl, Prodr. Monogr. Lobel. 28. 1836. *Dortmanna purpurea* (G. Don) Kuntze, Revis. Gen. Pl. 972. 1891. TYPE: CHILE. Valparaíso, Feb 1825, *MacRae s.n.* (LECTOTYPE [designated by Wimmer 1953: 616]: CGE; ISOLECTOTYPES: E! K!).

Rapuntium besserianum C. Presl, Prodr. Monogr. Lobel. 28. 1836. *Tupa besseriana* (C. Presl) A. DC. in DC., Prodr. 7:393. 1839. *Tupa polyphylla* var. *besseriana* (C. Presl) Vatke, Linnaea 38:727. 1874. *Dortmanna besseriana* (C. Presl) Kuntze, Revis. Gen. Pl. 972. 1891. *Lobelia polyphylla* var. *besseriana* (C. Presl) Reiche, Anales Univ. Chile 117:459. 1905. TYPE: CHILE. VALPARAÍSO, 2.1 km S of Punta de Angeles, on the coastal road from Valparaíso to Laguna Verde, steep rocky slopes of *quebrada* above the road, elev. 120 m, 2 Nov 1990, *Lammers, Baeza & Peñailillo 7741* (NEOTYPE here designated: F!; ISONEOTYPE: CONC!). As no original material could be located, a recent collection that agrees with the protologue is here selected to serve as the neotype.

Rapuntium subdentatum C. Presl, Prodr. Monogr. Lobel. 28. 1836. *Tupa subdentata* (C. Presl) A. DC. in DC., Prodr. 7:393. 1839. *Dortmanna subdentata* (C. Presl) Kuntze, Revis. Gen. Pl. 972. 1891. *Lobelia polyphylla* f. *subdentata* (C. Presl) E. Wimm., Pflanzenr. IV.276b:615. 1953. TYPE: CHILE. In cordilleris, *anonymous s.n.* (HOLOTYPE: PR!).

Rapuntium bracteosum C. Presl, Prodr. Monogr. Lobel. 29. 1836. *Tupa bracteosa* (C. Presl) A. DC. in DC., Prodr. 7:393. 1839. *Tupa polyphylla* var. *bracteosa* (C. Presl) Vatke, Linnaea 38:727. 1874. *Dortmanna bracteosa* (C. Presl) Kuntze, Revis. Gen. Pl. 972. 1891. *Lobelia polyphylla* var. *bracteosa* (C. Presl) Reiche, Anales Univ. Chile 117:459. 1905. *Lobelia polyphylla* f. *bracteosa* (C. Presl) E. Wimm., Ann. Naturhist. Mus. Wien 56:365. 1948. TYPE: CHILE. Quillota, fruticetis petrosis collium, Oct [1829], *Bertero 1103* (HOLOTYPE: PR!; ISOTYPES: BM[2]! GH[2]! M! NY! P! TUB! W!)

Rapuntium hyssopifolium C. Presl, Prodr. Monogr. Lobel. 29. 1836. *Tupa hyssopifolia* (C. Presl) A. DC. in DC., Prodr. 7:393. 1839. *Lobelia hyssopifolia* (C. Presl) C. Gay, Fl. Chile 326. 1849. *Dortmanna hyssopifolia* (C. Presl) Kuntze, Revis. Gen. Pl. 972. 1891. *Lobelia polyphylla* f. *hyssopifolia* (C. Presl) E. Wimm., Ann. Naturhist. Mus. Wien 56:365. 1948. TYPE: "Peruvia? Chile?", *anonymous s.n.* (HOLOTYPE: PR!).

Tupa polyphylla var. *angustifolia* Hook. & Arn. ex A. DC. in DC., Prodr. 7:393. 1839. *Lobelia polyphylla* var. *angustifolia* (Hook. & Arn. ex A. DC.) Heynh., Nom. Bot. Hort. 1:473. 1840. TYPE: CHILE. Prope Coquimbo, 1831, *Cuming 888* (LECTOTYPE here designated: K!; ISOLECTOTYPE: K!). The other syntype was *Bertero 110* (G-DC [microfiche!]).

Tupa polyphylla var. *latifolia* A. DC. in DC., Prodr. 7:393. 1839. *Lobelia polyphylla* var. *latifolia* (A. DC.) Heynh., Nom. Bot. Hort. 1:473. 1840. TYPE: CHILE. Prope Valparaíso, 1831, *Cuming 599* (LECTOTYPE here designated: K!; ISOLECTOTYPES: BM! CONC! E! GH! RSA! W!). The other syntype was *Poeppig 290* (G-DC [microfiche!]; ISOSYNTYPES: BM! W[3]!).

Tupa atropurpurea Vis., Ill. Piant. Nuov. 2:23. 1844. TYPE: CHILE. PROV. VALPARAÍSO: 3 km N of Laguna Verde, on the coastal road from Valparaíso, steep rocky slopes overlooking Bahia Laguna Verde, below the road, elev. 150–220 m, 2 Nov 1990, *Lammers, Baeza & Peñailillo 7760* (NEOTYPE here designated: F! ISONEOTYPES: CONC! MO!). Described from living plants cultivated at the botanic garden in Padua, Italy. As no original material could be located at PAD (R. Marcucci, in litt., 3 Dec 1997) or elsewhere, a recent collection that agrees with the protologue is designated as the neotype.

Tupa ovata Phil., Anales Univ. Santiago 43:506. 1873; non G. Don, Gen. Hist. 3:700. 1834. *Lobelia ovata* Reiche, Anales Univ. Chile 117:460. 1905. TYPE: CHILE. Carrizal bajo, Dec 1871, *King s.n.* (HOLOTYPE: SGO-043561 [three small branches on right side of sheet]!; ISOTYPES: BM! K!). The one large branch on the left side of the sheet is another specimen [Bandurrias, *Geisse s.n.*] which bears the manuscript name "Tupa glabrata Ph."

Tupa polyphylla var. *coquimbana* Vatke, Linnaea 38:727. 1874. *Lobelia polyphylla* var. *coquimbana* (Vatke) Reiche, Anales Univ. Chile 117:459. 1905. TYPE: CHILE. PROV. COQUIMBO [Elqui]: entrada al camino del Mineral La Hiquera, al norte de portezuelo de la Cuesta de Buenos Aires, 13 Oct 1963, *Marticorena & Matthei 172* (NEOTYPE here designated: CONC!; ISONEOTYPE: OS!). Because the original material presumably was destroyed during World War II (cf. Lammers 1994) and no duplicates could be found, a more recent gathering that conforms to the protologue is here designated as the neotype.

Tupa poeppigiana Phil., Anales Univ. Santiago 90:188. 1895. TYPE: CHILE. Quillota, *Germain s.n.* (LECTOTYPE here designated: SGO-057199!). No specimen was cited in the protologue, merely the locality "Quillota." The sheet designated as lectotype was the only one in Philippi's herbarium that agreed with the protologue and that was annotated with this name in his handwriting.

Tupa axilliflora Phil., Anales Univ. Santiago 90:188. 1895. *Lobelia axilliflora* (Phil.) Reiche, Anales Univ. Chile 117:460. 1895. TYPE: CHILE. Coquimbo, *Soza s.n.* (LECTOTYPE here designated: SGO-057182!). The other syntype cited in the protologue [Catemu, Sep 1860, *Philippi s.n.* (SGO-057183! [photograph: GH!]; ISOSYNTYPE: W!)] was never annotated by Philippi with this name. Although Muñoz (1960) cited both localities, only the accession number of the latter was listed.

Tupa gayana Phil., Anales Univ. Santiago 90:189. 1895. TYPE: CHILE. PROV. COQUIMBO: ad rivulos Serena, Oct 1836, *Gay 1466* (HOLOTYPE: SGO! [photograph: GH!]).

Tupa linearifolia Phil., Anales Univ. Santiago 90:189. 1895. *Lobelia polyphylla* f. *linearifolia* (Phil.) E. Wimm., Ann. Naturhist. Mus. Wien 56:365. 1948. TYPE: CHILE. Coquimbo, 1889/90, *Geisse s.n.* (LECTOTYPE here designated: SGO-057195!). No specimen was cited in the protologue, merely the locality "Coquimbo." Philippi's herbarium contains three sheets that matched the protologue reasonably well (Muñoz 1960). The specimen here designated as the lectotype was the only one annotated with this name in Philippi's handwriting.

Tupa serrata Phil., Anales Univ. Santiago 90:189. 1895. TYPE: CHILE. Valparaíso, *King s.n.* (HOLOTYPE: SGO-057185![photograph: GH!]).

Shrubs, 0.6–2 m tall; stems woody, repeatedly branched, solid, pubescent or glabrous; latex white. Lamina 1.8–16 cm long, 0.4–4.8 cm wide, ovate, widely ovate, narrowly oblong, widely elliptic, elliptic, narrowly elliptic, lanceolate, or linear, minutely pubescent or glabrous; margin entire, denticulate, serrulate, or serrate; apex rounded, obtuse, acute, acuminate, or long acuminate, sometimes mucronate, cuspidate, or aristate; base trun-

cate, rounded, obtuse, cuneate, or attenuate. Flowers solitary in the axils of the upper leaves, or aggregated into a 10–30(–45)-flowered raceme; bracts 7–50(–75) mm long, 2.5–28 mm wide, widely elliptic, elliptic, narrowly elliptic, lanceolate, or ovate, glabrous or minutely pubescent; pedicels 7–17 mm long, ebracteolate (very rarely some with a pair of linear bracteoles 2–5 mm long at or below the middle), minutely pubescent. Hypanthium 4–7 mm long, 4–8 mm in diameter, obconic, campanulate, or rarely obovoid, pubescent or subglabrous. Calyx lobes 3–8 mm long, 1–3 mm wide, triangular or narrowly triangular, pubescent; margin entire or very rarely with a few teeth; apex acuminate or long acuminate. Corolla 15–25 mm long, wine-purple, minutely pubescent; tube (7–)10–17 mm long, 1.5–3 mm in diameter at middle, suberect or curved; lobes 4–12 mm long, 0.8–2 mm wide. Filament tube 9–15 mm long, purple; anther tube 4–7 mm long, 1.2–2.5 mm in diameter, grey with pale stripes, glabrous or the dorsal three rarely with scattered long pubescence. Capsule 9–12 mm long, 6–9 mm in diameter, broadly ellipsoid or ovoid. Seeds 0.7–1 mm long, 0.3–0.4 mm in diameter, oblong or ellipsoid, light brown or golden brown, faintly striate (Murata 1995, figs. 52–53). Chromosome number $n = 21$ (Lammers & Hensold 1992; Lammers 1993a).

Icones.—Lindley (1830) [as *L. purpurea*]; D. Don (1834); Hooker (1837); Loudon (1844), pl. 66, fig. 3; Navas (1979), pl. 42D–G.

Distribution, Habitat, and Phenology.—Endemic to xeric north-central Chile between latitude 27°S and 34°S, in the regions of dwarf- and xerophytic-shrub and sclerophyllous vegetation (cf. Walter 1973). Frequent on dry rocky slopes and cliffs, sometimes in sandy soil, from near sea level (often in sight of the ocean) up to 900 m, rarely as high as 1200 m above sea level, often in company with *L. excelsa*. Flowering August through February.

Discussion.—This species is extremely variable in foliar features, especially size and shape of the lamina and the degree of reduction in leaves subtending flowers (i.e., whether the plant forms a discrete bracteate inflorescence or bears solitary flowers in axils of unreduced leaves). This inordinate variability is the source of the species' extensive synonymy. Though the extremes [e.g., plants distinguished by Wimmer (1953) as *L. polyphylla* f. *linearifolia* and *L. ovata*] appear most distinct, it was noted during field study that many populations were quite heterogeneous in foliar morphology. Individuals that differed considerably in leaf length, width, and outline often were found growing side-by-side. Furthermore, leaves that emerged and expanded early in the season often differed significantly from those appearing later. In some cases, two or three of Wimmer's "taxa" could be found on a single individual. For example, in *Marticorena et al. 1367* (CONC), the lower leaves key to var. *besseriana* while the upper leaves key to var. *latifolia*. This suggests that at least some of the observed variation is environmentally induced (related to rainfall or day-length perhaps) rather than under genetic control, or perhaps related to heteroblasty.

In detailed multivariate analyses of this species (Lammers & Glass 1998), no patterns were discernible in the data, which were gathered from 64 herbarium sheets, including nearly all type specimens. Variation in foliar features was absolutely continuous,

with no gaps by which meaningful taxa (including *L. ovata*) could be distinguished. No correlations were detected between foliar morphology and any geographic, ecologic, or elevational parameters. Furthermore, the plants examined cytologically (Lammers & Hensold 1992) well represented the diversity of foliar morphology; all showed $n = 21$.

In contrast to foliar structures, the flowers of *L. polyphylla* are remarkably homogeneous. They are distinctive within the section because of their small size and the dark pigmentation. The hue of the corolla is a very intense red-purple which compares favorably to the color of a good Chilean red wine ("vino tinto"). The only variation in floral features which appeared to be geographically correlated was anther pubescence, which showed a clinal pattern of variation: pubescent anthers were commonest towards the north, glabrous anthers towards the south.

This species is unusual among Lobelioideae in showing some variability in the presence or absence of bracteoles. However, the single specimen found that had bibracteolate pedicels (*Marticorena et al. 1379,* CONC) also showed typical ebracteolate pedicels in the same inflorescence. Similarly, inflorescences in sect. *Tupa* ordinarily are anauxotelic (i.e., incapable of renewing vegetative growth; cf. Stein 1987), with growth resuming via branching from axillary buds below the spent inflorescence. However, one collection (*Schlegel 2752,* CONC, SGO) was seen that was clearly auxotelic, with an inflorescence in full anthesis surmounted by ca. 15 cm of new vegetative growth.

Representative specimens. **CHILE. Prov. Copiapó:** 20–25 km W of Totoral, *Taylor et al. 10807* (ASU, MO). **Prov. Huasco:** Las Lozas, *Böcher et al. 545* (C); Huasco, *Kubitzki 290* (VALD); Mina Los Cristales, *Marticorena et al. 1700* (CONC); Huasco, *Montero 7611* (CONC, OS); Quebrada del Pretil, *Ricardi & Marticorena 3966* (CONC); 3–4 km SW of Huasco, *Worth & Morrison 16245* (GH, UC). **Prov. Elqui:** Punta Arrayan, *Dillon et al. 5437* (F); La Higuera, Jan 1886, *Fonck s.n.* (SGO); La Serena, *Frödin 153* (UPS); entre La Serena y Vallenar, *Garaventa 4241* (CONC); entre Tongoy y Guanaqueros, *Gleisner 14* (CONC); El Tofo, *Kubitzki 279* (CONC, VALD); Punta Herradura, *Lammers 7650* (ASC, CONC, F, MU, OSH, UC, US); Punta Teatinos, *Landrum & Landrum 5634* (ASU, GH, NY, RSA, UC); Coquimbo, Oct 1878, *Philippi s.n.* (SGO); La Serena, Sep 1898, *Reiche s.n.* (SGO); Cuesta de las Cordas, *Ricardi & Marticorena 4564/949* (CONC, OS); 20 km S of Incahuasi, *Ricardi & Marticorena 4896/1281* (CONC, OS, Universidad de Talca); La Serena, *Sparre 2793* (S, SGO); N of La Serena, *Taylor et al. 10654* (ASU, F, MO). **Prov. Límarí:** Talinay, *Jiles 439* (CONC); Fray Jorge, *Kubitzki 100* (VALD); 1 km N of Mantos de Hornillo, *Lammers et al. 6372* (CONC, F); 11 km N of Mantos de Hornillo, *Lammers et al. 6386* (CONC, F), *6389* (B, CONC, F, MU), *7665* (CONC, F), *7666* (CONC, F); Fray Jorge, *Muñoz B-152* (SGO); Fray Jorge, *Skottsberg & Skottsberg 887* (GB, NY, S); Fray Jorge, *Werdermann 901* (A, B, BM, E, F, GH, M, MO, NY, UC, US). **Prov. Choapa:** Pichidangui, *Correa 67* (SGO); Puente Negro, *Jiles 4354* (CONC); 0.2 km N of Los Vilos, *Lammers et al. 6331* (B, C, CONC, GB, F, MEXU, MU); 7 km N of Los Vilos, *Lammers et al. 6341* (CONC, F, MU, NY); 8.9 km N of Los Vilos, *Lammers et al. 7536* (CONC, F, TEX); 8.3 km N of Puerto Oscuro, *Lammers et al. 7668* (B, CONC, F, TEX); 23.6 km S of Los Vilos, *Lammers et al. 7677* (CONC, F, MU, OSH, US); Estacion Ingenerio Barriga, *Marticorena et al. 210* (CONC); Agua Amarilla, *Marticorena et al. 332* (B); N of Los Vilos, *McGill 1028* (ASU); Illapel, *Rose & Rose 19241* (NY, US); 33 km SW of Illapel, *Worth & Morrison 16646* (BH). **Prov. Petorca:** 4 km N of Longotoma, *Lammers et al. 6397* (CONC, F, MU, OS, UB); 1 km. S of Papudo, *Lammers et al. 6402* (CONC, F, MU); 1.3 km N of northernmost road to Zapallar, *Lammers et al. 7700* (CONC, F). **Prov. San Felipe de Aconcagua:** Quebrada de Las Palmas, Sep 1965, *Ramirez s.n.* (VALD). **Prov. Valparaíso:** Limache, *Garaventa 299* (CONC); Valparaíso, *Gaudichaud 129* (CONC); Concon, *Gunckel 19081* (CONC); Renaca, *Jaffuel 1752* (CONC); Quintero, *Lammers et al. 6412* (CONC, F), *6413* (CONC, F),

6414 (F), *6415* (F), *7723* (ASC, CONC, F), *7724* (CONC, F), *7725* (BM, CONC, F, UC); 2.6 km S of Punta de Angeles, *Lammers et al. 7753* (CONC, F, NY, OS); Mirasol, *Landrum 3821* (MICH, MO, NY, SGO); Valparaíso, Dec 1851, *Philippi s.n.* (SGO); Placeres, *Stebbins 8542* (UC); Quintero, *Werdermann 30* (BM, CAS, E, F, GH, M, MO, S, U, UC, US). **Prov. San Antonio:** El Tabo, *Gunckel 25483* (CONC); Algarrobo, *Lammers et al. 7800* (B, CONC, F); Quebrada de Cordoba, Jan 1980, *Navarreto s.n.* (VALD). **Región Metropolitana:** Tejas Verdes, *Gunckel 24556* (CONC); Pentaflor, *Montero 1748* (CONC); Cartagena, *Navas 2298* (CONC); Dunas de Las Cruces, 19 Oct 1950, *Pfister & Ricardi s.n.* (CONC, OS).

CULTIVATION. U.S.A. California: University of California Botanical Garden, Berkeley, Jul 1963, *Hutchinson s.n.* (MICH).

2. Lobelia excelsa Bonpl., Descr. Pl. Malmaison 112. 1816. *Rapuntium excelsum* (Bonpl.) C. Presl, Prodr. Monogr. Lobel. 29. 1836. *Dortmanna excelsa* (Bonpl.) Kuntze, Revis. Gen. Pl. 972. 1891. TYPE: FRANCE. Hort. Malmaison, Jun 1813 (LECTOTYPE here designated: Bonpland 1816, pl. 46!). As no original material was located, the plate published with the protologue is here designated as the lectotype.

Lobelia gigantea Sims, Bot. Mag. 32:pl. 1325. 1810; non Cav., Anales Hist. Nat. 2:104. 1800. *Lobelia salicifolia* Sweet, Hort. Suburb. Lond. 37. 1818. *Tupa salicifolia* (Sweet) G. Don, Gen. Hist. 3:700. 1834. TYPE: CHILE. Valparaíso, 1794, *Menzies s.n.* (LECTOTYPE here designated: BM! ISOLECTOTYPE: MO!). The name was based on this collection and on living plants growing in a commercial nursery.

Lobelia arguta Lindl., Edwards' Bot. Reg. 12:pl. 973. 1826. *Tupa arguta* (Lindl.) G. Don, Gen. Hist. 3:700. 1834. *Dortmanna arguta* (Lindl.) Kuntze, Revis. Gen. Pl. 972. 1891. TYPE: GREAT BRITAIN. Chiswick Garden, Sep 1825 (LECTOTYPE here designated: Lindley 1826, pl. 973!). As no original material was located, the plate published with the protologue is here designated as the lectotype.

Lobelia neriifolia Moris, Enum. Sem. Hort. Bot. Taurin. 1833:20. 1833. TYPE: CHILE. PROV. CARDENAL CARO: 1.2 km E of Pichilemu on highway to Nancagua, frequent on arid rocky bluffs above the road, elev. 45 m, 15 Nov 1990, *Lammers, Baeza & Peñailillo 7890* (NEOTYPE here designated: OSH!; ISONEOTYPES: CONC! F! MU! TEX! US!). Described on the basis of living plants grown in the botanic garden at Turin, Italy, from seeds sent by Bertero. As no original material or Bertero specimens could be located, a recent collection that conforms to the protologue is here designated as the neotype.

Tupa glaucescens Phil., Anales Univ. Santiago 90:187. 1895. TYPE: CHILE. San Isidrio, Dec 1882, *Philippi s.n.* (HOLOTYPE: SGO!).

Shrubs, 2–4 m tall, rarely trees to 6.8 m; stems woody, repeatedly branched, solid, glabrous or minutely pubescent; latex tan or pale yellow. Lamina 2.8–15 cm long, 0.7–3.1 cm wide, oblong, narrowly oblong, elliptic, or narrowly elliptic, rarely lanceolate, glabrous or minutely pubescent; margin serrulate, minutely serrulate, or subentire; apex obtuse, acute, or acuminate, sometimes cuspidate, mucronate, or aristate; base rounded, obtuse, cuneate, or attenuate. Flowers solitary in the axils of the upper leaves; pedicels 12–45 mm long, bibracteolate on the lower third or rarely at the middle, minutely pubescent; bracteoles 2.5–10 mm long, linear, minutely pubescent. Hypanthium 5–10 mm long, 8–15 mm in diameter, hemispheric, broadly hemispheric, broadly campanulate, obconic, or broadly obconic, glabrous or minutely pubescent. Calyx lobes 3.5–9(–20) mm long, 1–4 mm wide, triangular or narrowly triangular, minutely pubescent; apex acuminate or long acuminate. Corolla (38–)45–65 mm long, yellow and orange in bud, becoming red at anthesis (very rarely all yellow), glabrous or sparsely pubescent with minute hairs; tube 25–42 mm long, 2.5–6 mm in diameter at middle, suberect or curved; lobes 12–33 mm

long, 1–3 mm wide. Filament tube 29–47 mm long, red; anther tube 8–11 mm long, 2–4 mm in diameter, pale straw-colored, the dorsal three with long white hairs on the surface (especially toward apex). Capsule 10–15 mm long, 11–18 mm in diameter, ovoid, obovoid, oblate, or subspherical. Seeds 1 mm long, 0.4 mm wide, oblong, honey-colored, faintly striate (Murata 1992, figs. 49–50, 70). Chromosome number $n = 21$ (Lammers & Hensold 1992; Lammers 1993a).

Icones.—Sims (1810) [as *L. gigantea*]; Bonpland (1816), pl. 46; Lindley (1826) [as *L. arguta*]; Muñoz (1966), pl. 128 [as *L. tupa*]; Navas (1979), pl. 42A–C [as *L. salicifolia*]; Hoffmann (1997), pg. 218 no. 1 [as *L. tupa*].

Distribution, Habitat, and Phenology.—Endemic to xeric north-central Chile between latitude 29°S and 35°S, in the regions of dwarf- and xerophytic-shrub and sclerophyllous vegetation (cf. Walter 1973). Frequent on dry rocky slopes and cliffs, sometimes in sandy soil, from near sea level (though seldom in sight of the ocean) up to 1200 m above sea level, often in company with *L. polyphylla*. Flowering September through February.

The report of this species from Bolivia (Wimmer 1953) is apparently due to an inadvertant switching of labels. *Rusby 623* (US) allegedly represents the only known specimen of *L. excelsa* from Bolivia, while *Rusby 634* (US) is supposedly the only specimen from Chile of another lobelioid, *Centropogon cornutus* (L.) Druce, which is indigenous to Bolivia (cf. Stein 1987). However, duplicates of *Rusby 634* at GH and NY are specimens of *L. excelsa* from Valparaíso. Clearly, labels were accidentally switched at some point, resulting in the erroneous reports.

Discussion.—In contrast to *L. polyphylla*, the other woody member of the section, *L. excelsa* is relatively homogeneous in its vegetative morphology. One feature that does vary more in this species than in *L. polyphylla* is habit. Although *L. excelsa* is ordinarily a shrub, one individual was encountered in Prov. Limarí in 1989 (*Lammers et al. 6382*, B, C, CONC, F, MU) that was definitely a tree. The plant was fully 6.8 m tall and did not begin to branch until 2.5 m above the ground. Its twin boles were 11.5 cm and 9.5 cm in diameter just above the base and were of sufficient strength that the tree could be climbed to collect flowering branches without damage.

Lobelia excelsa is unique within the section in its tan or pale yellow (vs. white) latex, regularly bibracteolate pedicels, and for the color change of its flowers, which go from yellow and orange in bud to brilliant red at full anthesis. The taxonomic distribution and biological significance of such color changes were detailed by Weiss (1995).

Plants bearing pure sulfur yellow flowers with no trace of orange or red (and thus no color change) are known, but only from cultivation. The label of a specimen cultivated in Switzerland [*anonymous s.n.*, 29 Jul 1858 (NY)] states "flor sulphurei." More recently, Eric Knox (pers. comm.) reported that plants grown at the University of Michigan's Matthei Botanical Garden from seed of *Lammers et al. 6393* consistently bore yellow flowers over a period of three years. I know for a fact that the plants from which the seed was obtained bore normally pigmented flowers. It would be of interest to learn if plants with yellow flowers ever occur in natural populations, and if so, under what conditions.

Representative specimens. **CHILE. Prov. Elqui:** Coquimbo, 14 Jan 1971, *Blaise s.n.* (SGO); Cuesta de Buenos Aires, *Kubitzki 278* (VALD); Cuesta de Buenos Aires, *Lammers et al. 7604* (ASC, CONC, F, OS, UC); Yerba Loca, *Simon 327* (RSA, UC); La Serena, *Sparre 2780* (S, SGO); 42 km N of La Serena, *Worth & Morrison 16328* (BH). **Prov. Limarí:** Monte Redondo, *Jiles 372* (CONC); Quebrada La Higuera, *Jiles 1131* (CONC); Cabreria, *Jiles 1150* (CONC); Fray Jorge, Sep 1958, *Kummerow s.n.* (CONC); 1 km N of Mantos de Hornillo, *Lammers et al. 6375* (CONC, F, MU, NY); 11 km N of Mantos de Hornillo, *Lammers et al. 7664* (BM, CONC, F). **Prov. Choapa:** 1 km S of Los Vilos, *DeVore 1574* (OSH); 0.2 km N of Los Vilos, *Lammers et al. 6330* (C, CONC, F, MEXU, MU, NY); 10 km N of Los Vilos, *Lammers et al. 6348* (CONC, F, MU, NY); 11 km E of Panamerican Hwy on road to Canela Baja, *Lammers et al. 6353* (CONC, F, GB, MU, NY); 5 km S of Canela Baja, *Lammers et al. 6357* (B, CONC, F, GB, MU); 8 km NE of Illapel, *Lammers et al. 6362* (CONC, F, MU); 7 km SE of Illapel, *Lammers et al. 6364* (CONC, F, NY); 24 km SW of Illapel, *Lammers et al. 6367* (B, CONC, F, MU); 6 km S of Puente Amolanas, *Lammers et al. 6370* (CONC, F, MU, NY); 14.5 km S of Río Choapa bridge, *Lammers et al. 7676* (CONC, F, NY); entre Illapel & Los Vilos, *Marticorena & Matthei 427* (CONC); Illapel, *Montero 2399* (CONC); Los Vilos, *Montero 8772* (CONC), *Montero 10777* (CONC); Illapel to Huentelauquen, *West 3940* (GH, MO, UC). **Prov. Petorca:** 3 km S of Zapallar, *Gardner & Page 5085* (E); Pichicuy, *Lammers et al. 6393* (B, CONC, F, MU); 2 km E of Papudo, *Lammers et al. 6399* (B, CONC, F, MU); 1 km S of Papudo, *Lammers et al. 6401* (B, CONC, F, MU); 21 km N of Nogales, *Lammers et al. 6408* (CONC, F, MU, NY); 14 km N of Nogales, *Lammers et al. 6411* (CONC, F, MU, NY); 1.3 km N of northernmost road to Zapallar, *Lammers et al. 7701* (ASC, CONC, F); Pichicuy, *Marticorena et al. 177* (CONC); Papudo, *Montero 8023* (CONC); Cerro Iman, *Villagran & Meza 750* (SGO), *932* (SGO). **Prov. San Felipe de Aconcagua:** Quebrada de Cabildo, 29 Jan 1950, *Pfister s.n.* (CONC, OS); Quebrada de Las Palmas, Sep 1965, *Ramirez s.n.* (VALD). **Prov. Quillota:** 12 km from Tiltil towards Olmue, *Gardner & Knees 5446* (E); Olmue, *Böcher et al. 587* (C); 2 km S of San Pedro, *Lammers et al. 6418* (CONC, F, MU, NY, UB); Parque Nacional La Campana, *Lammers et al. 6440* (B, CONC, F, MU), *6448* (CONC, F, MU), *6450* (CONC, F, MU), *6452* (CONC, F). **Prov. Valparaíso:** Valparaíso, *Gaudichaud 129* (P); Las Zonas, *Harshberger 1074* (NY, PENN); Quebrada de la Tortuga, 24 Feb 1941, *Junge s.n.* (CONC, OS); 9 km N of Concon, *Lammers et al. 6417* (CONC); 2.6 km S of Punta de Angeles, *Lammers et al. 7754* (CONC, F, UC); 3 km N of Laguna Verde, *Lammers et al. 7759* (CONC, F); Algarrobo, *Landrum 3341* (ASU); Mirasol, *Landrum 3822* (MICH, NY, SGO); Quebradas de Viña, *Lourteig 2510* (K, S); El Salto, *Meyer 9336* (MO, UC); Valparaíso, Dec 1862, *Philippi s.n.* (SGO); Via del Mar, *Ricardi 5449* (CONC); Valparaíso, *Rusby 634* (K, MICH, NY, PH); Valaparaíso, *Rusby 634* (GH, NY); Agua Potable, *Schlegel 381* (CONC); Cerro Valparaíso, *Schlegel 967* (CONC); Quebrada Verde, *Schlegel 89* (CONC); El Salto, *Skottsberg & Skottsberg 947* (GB, S); El Salto, *Solbrig et al. 3600* (GH, NY); 3.9 km N of Concon, *Spooner & Contreras 4304* (CONC, F, MO, WIS). **Prov. San Antonio:** Quebrada Cordoba, *Gentry 68043* (NY); 3 km E of Algarrobo, *Lammers et al. 7795* (B, BM, CONC, F); N of San Sebastian, 2 Feb 1971, *Oehrens s.n.* (VALD); El Tabo, Feb 1968, *Santos s.n.* (VALD). **Región Metropolitana:** Quebrada Dormida, *Garaventa 1323* (CONC); Cerro La Cruz, 30 Sep 1932, *Olathe s.n.* (CONC); Dunas de las Cruces, 19 Oct 1950, *Pfister & Ricardi s.n.* (CONC, OS); Quebrada La Plata, *Schlegel 1680* (CONC). **Prov. Cardenal Caro:** Pichilemu, *Montero 9286* (CONC); 9 km S of Pichilemu, *Lammers et al. 7903* (CONC, F, MO, NY); Estuario Nilahue, *Lammers et al. 7917* (CONC, F, NY); 4.2 km N of Bucalemu, *Lammers et al. 7933* (CONC, F); Pichilemu, *Sanz de Cortazar 573* (SGO). **Prov. Colchagua:** Ciruelos, *Aravena 47* (SGO); Matanzas, Mar 1878, *Fernández s.n.* (SGO); Nancagua, 11 Jan 1951, *Ricardi s.n.* (CONC, OS). **Prov. Curicó:** Lipimavida, *Aravena 34L* (SGO); Lipimavida, *Spooner & Contreras 4332* (CONC, F, WIS); Punta Totorilla, 6 Feb 1969, *Villagran & Tapia s.n.* (SGO); 1 km antes de Iloca, *Weldt 107* (CONC). **Prov. Talca:** Quivolgo, *Matthei & Bustos 34* (B); Constitución, Feb 1895, *Philippi s.n.* (SGO).

CULTIVATION. SWITZERLAND: Hort. Bot. Basil., 29 Jul 1858, *anonymous s.n.* (NY).

3. Lobelia tupa L., Sp. Pl. 929. 1753, 'trapa.' *Tupa feuillei* G. Don, Gen. Hist. 3:700. 1834. *Rapuntium tupa* (L.) C. Presl, Prodr. Monogr. Lobel. 28. 1836. *Dortmanna tupa* (L.) Kuntze, Revis. Gen. Pl. 972.

1891. *Lobelia feuillei* (G. Don) Voss in Siebert & Voss, Vilm. Blumengärtn. (ed. 3) 1:577. 1894, nom. illeg. TYPE: CHILE. Mountains, 37°S (LECTOTYPE [designated by Matthews 1988:161]: Feuillée 1714, pl. 29!).

Lobelia mucronata Cav., Icon. 6:11. 1801. *Tupa cavanillesiana* G. Don, Gen. Hist. 3:700. 1834, nom. illeg. *Rapuntium mucronatum* (Cav.) C. Presl, Prodr. Monogr. Lobel. 29. 1836. *Tupa mucronata* (Cav.) A. DC. in DC., Prodr. 7:392. 1839. *Tupa feuillei* var. *mucronata* (Cav.) Vatke, Linnaea 38:727. 1874. *Dortmanna mucronata* (Cav.) Kuntze, Revis. Gen. Pl. 972. 1891. *Lobelia tupa* var. *mucronata* (Cav.) Reiche, Anales Univ. Chile 117:458. 1905. TYPE: CHILE. Fundo Cuchacucha, *Nee s.n.* (HOLOTYPE: MA! [photographs: F! GH! MICH! W!; fragments: F! CONC! W!]).

Lobelia serrata Meyen, Reise 1:300. 1834. TYPE: CHILE. PROV. CURICÓ: Hacienda Monte Grande, alt. ca. 600 m, Dec 1924, *Werdermann 572* (NEOTYPE here designated: BM!; ISONEOTYPES: E! F! GH! M! MO! NY! UC!). No original material could be located, so a more recent collection from the same general area, which agrees with the protologue, is here designated as the neotype.

Tupa berteroi A. DC. in DC., Prodr. 7:392. 1839, 'berterii.' *Tupa feuillei* var. *berteroi* (A. DC.) Vatke, Linnaea 38:727. 1874, 'berterii.' *Dortmanna berteroi* (A. DC.) Kuntze, Revis. Gen. Pl. 972. 1891. *Lobelia tupa* var. *berteroi* (A. DC.) Reiche, Anales Univ. Chile 117:458. 1905, 'berterii.' *Lobelia mucronata* var. *berteroi* (A. DC.) E. Wimm., Pflanzenr. IV.276b:614. 1953, 'berterii.' TYPE: CHILE. Rancagua, in sylvaticis umbrosis, torrentes et rivulos, Apr 1828, *Bertero 389* (HOLOTYPE: G-DC [microfiche!]; ISOTYPES: P! SGO!). Orthography corrected following the recommendations of Stuessy and Marticorena (1990).

Tupa mucronata var. *hookeri* A. DC. in DC., Prodr. 7:392. 1839. *Lobelia mucronata* f. *hookeri* (A. DC.) E. Wimm., Pflanzenr. IV.276b: 614. 1953. TYPE: GREAT BRITAIN. Scotland, Glasgow Botanic Garden, Aug 1832 (HOLOTYPE: Hooker 1833, pl. 3207!).

Tupa montana Phil., Anales Univ. Santiago 43:506. 1873; non C. Wright ex Griseb., Cat. Pl. Cub. 159. 1866. *Dortmanna philippiana* Kuntze, Revis. Gen. Pl. 972. 1891. *Lobelia tupa* var. *montana* Reiche, Anales Univ. Chile 117:459. 1905. TYPE: CHILE. Hac[ienda]. del Principal, 1870, *Philippi s.n.* (HOLOTYPE: SGO-057202!; ISOTYPE: SGO-043568! [photograph: GH!]).

Tupa feuillei var. *macrophylla* Vatke, Linnaea 38:726. 1874. TYPE: GREAT BRITAIN. Lowe's Nursery (LECTOTYPE here designated: Lindley 1833, pl. 1612!). Vatke also cited *Philippi 340, Ochsenius s.n.*, and a specimen cultivated at Berlin in 1832, all deposited at B. None of these specimens could be located and presumably perished during World War II (cf. Lammers 1994). I have seen duplicates of the Philippi specimen at K, P, and W, but they do not conform to the description given in the protologue, while the plate does.

Dortmanna bicalcarata Kuntze, Revis. Gen. Pl. 3(2): 186. 1898. *Lobelia bicalcarata* (Kuntze) A. Zahlbr. ex K. Schum., Just's Bot. Jahresber. 26(1): 373. 1900. *Lobelia tupa* var. *bicalcarata* (Kuntze) E. Wimm., Ann. Naturhist. Mus. Wien 56:365. 1948. TYPE: CHILE. Chiguayante, 19 Feb 1892, *Kuntze s.n.* (HOLOTYPE [mounted on two sheets]: NY!; ISOTYPES: B† [photographs: F! GH! MICH! NY! SGO!], W! [photographs: A! F! MICH!]).

Lobelia mucronata f. *ovalifolia* E. Wimm., Pflanzenr. IV.276b:614. 1953. TYPE: GERMANY. H[ort.] Bonn, 1848, *anonymous s.n.* (HOLOTYPE: B!).

Lobelia tupa var. *pavonii* E. Wimm., Pflanzenr. IV.276c: 881. 1968. TYPE: CHILE. *Ruiz & Pavon s.n.* (HOLOTYPE: BM!).

Robust perennials, 0.5–3 m tall; stems several from the base, normally unbranched, hollow, herbaceous or suffruticose, densely short or long pubescent; latex white. Lamina 4.5–25.5 cm long, 1.2–7.8 cm wide, ovate, oblong, elliptic, narrowly elliptic, or rarely lanceolate; upper surface densely short pubescent; lower surface very densely short pubescent; margin serrulate or minutely serrulate; apex acute or acuminate, sometimes

mucronate or cuspidate; base sagittate, the pair of basal lobes decurrent on the stem for 2–30 mm (rarely cuneate or obtuse and non-decurrent). Inflorescence a 10–65-flowered raceme, densely short pubescent; bracts 7–45(–85) mm long, 2–15(–20) mm wide, ovate, lanceolate, or rarely linear, the apex acuminate, the base sagittate, the pair of basal lobes decurrent on the stem for 2–33 mm (or very rarely free from the stem), rarely obtuse and non-decurrent; pedicels 8–30 mm long, ebracteolate. Hypanthium 5–10 mm long, 8–14 mm in diameter, hemispheric, depressed hemispheric, obconic, or broadly campanulate, densely short pubescent. Calyx lobes 2–8 mm long, 1–3 mm wide, triangular or narrowly triangular, short pubescent; apex acuminate, long acuminate, or rarely acute. Corolla 31–49 mm long, red (very rarely yellow), sparsely or densely short pubescent; tube 19–35 mm long, 2–4 mm in diameter at middle, arcuate; lobes 10–22 mm long, 1–2.5 mm wide. Filament tube 22–33 mm long, red; anther tube 6–9 mm long, 2–3 mm in diameter, grey, the dorsal three pubescent with long white hairs or rarely glabrous. Capsule 0.9 cm long, 1.2 cm in diameter, ovoid. Seeds 0.7 mm long, 0.3 mm wide, broadly ellipsoid, honey-brown, minutely foveolate-reticulate (Murata 1995, figs. 54–55). Chromosome number $n = 21$ (Vilmorin & Simonet 1927; Spooner et al. 1987; Lammers & Hensold 1992; Lammers 1993a); the voucher (*Sanz 573*, SGO) for Sanz de Cortazar's (1948) report of $n = 16$ in *L. tupa* is actually a specimen of *L. excelsa*, and the count is considered erroneous in any event (Lammers & Hensold 1992; Lammers 1993a).

Icones.—Feuillée (1714), pl. 29 [as "Rapuntium spicatum ..."]; Cavanilles (1801), pl. 516 [as *L. mucronata*]; Sims (1825); Sweet (1827–29); Hooker (1833) [as *L. mucronata*]; Lindley (1833); Loudon (1844), pl. 66, fig. 1; Santa Cruz (1932), p. 99; Wimmer (1953), fig. 96; Finnis (1966), fig. 48; Schultes (1976), p. 153, (1981), p. 122; Matthews (1988); Thomas (1990), pl. II, no. 5; Hoffmann (1997), pg. 218, no. 2 [as *L. bridgesii*].

Distribution, Habitat, and Phenology.—Endemic to mesic south-central Chile between latitude 32°S and 42°S, in the regions of deciduous forest and evergreen temperate rain forest (cf. Walter 1973). Also naturalized on Masatierra (Isla Robinson Crusoe) in the Juan Fernández Islands sometime prior to 1824 (Matthei et al. 1993). Common on roadsides, fields, streambanks, grassy slopes, and forest margins, at elevations from near sea level up to 400 m (rarely up to 940 m). Flowering late October to early April.

Discussion.—*Lobelia tupa* varies considerably in the nature of its leaf and bract bases, variation which Wimmer (1953) used to recognize several taxa. Typically, the leaf margins continue as a pair a broad triangular auricles for some distance below the point of attachment of the midrib at the node, forming a sagittate base that is adnate to the stem. Wimmer (1953, 1968) treated plants with relatively short auricles, particularly among the bracts, as var. *tupa* or (if the leaves were lanceolate) var. *pavonii*. Those with very long auricles were var. *montana* or (if the auricles of the bracts were free from the inflorescence rachis) var. *bicalcarata*. Otherwise similar plants with obtuse or cuneate non-decurrent leaf bases were segregated as *L. mucronata*. Plants that were intermediate between *L. mucronata* and *L. tupa*, i.e., those with very shortly decurrent auricles, were treated as *L. mucronata* var. *berteroi*. The intermediacy of this variety is highlighted by the fact that Vatke (1874) and Reiche (1905, 1910) previously had assigned it to *L. tupa*.

Careful study of natural populations showed that the length of the basal auricles varied considerably within populations and even within individual plants. This was apparent even in herbarium material. In *Gay 1468* (SGO), the auricles were only 3 mm long in the basal-most leaves, but 15 mm long within the inflorescence. As such, the varieties of *L. tupa* recognized by Wimmer (1953, 1968) do not merit recognition.

The case of *L. mucronata* is more complex. Though not emphasized by Wimmer, it differs from *L. tupa* not only in it non-decurrent leaves, but also in its very sparse inflorescence (cf. Hooker 1833). Here, only 10–15 flowers form before the apical meristem aborts; the flowers appear to be largely in bloom all at once and to take on a nodding rather than spreading or ascending posture. However, all other features of the plants, including the flowers and the seeds, are identical to *L. tupa*. Furthermore, all specimens referable to *L. mucronata* have been collected within the geographic and elevational range of *L. tupa*.

I was unable to locate plants in nature that matched this description, and have seen only a few specimens besides the types cited above. While it is possible that *L. mucronata* is an extremely rare or possibly extinct species, perhaps adapted to some unusual edaphic niche, other hypotheses must be considered. The handful of specimens examined may simply represent plants of *L. tupa* whose apical meristems were damaged at a critical point of development by some insect or pathogen, resulting in aberrant growth. They may represent an occasional genetic variant, perhaps a simple Mendelian recessive, of that species. Alternatively, these plants may be relicts close to the evolutionary divergence of *L. excelsa* and *L. tupa*, or recent hybrids of these two species. Although they are not sympatric today, their ranges do approach one another (see above) and may have overlapped in the past. The most recent gathering of plants referable to *L. mucronata* (*Montero 736*, CONC) was collected in 1928 in Prov. Colchagua, in the zone of closest approach between these two species.

Until such time as sufficient new data permit support or rejection of some of these hypotheses, I am loathe to recognize *L. mucronata* as a distinct species. Because it occurs within the geographic range of *L. tupa* and because its flowers and seeds are indistinguishable from those of that species, it is here relegated to synonymy.

Populations of *L. tupa* also show clinal variation in pubescence. The hairs on leaves and stems generally become longer and softer from north to south, while the dorsal surface of the anther tube becomes increasingly pubescent from south to north. The corolla of *L. tupa* typically is red, though it does not change color (Weiss 1995) as in *L. excelsa*. I have seen just one specimen (*Reiche s.n.*, Jan 1902, SGO) in which the corolla is yellow ("flores flavescente"; cf. Reiche 1905, 1910).

Representative specimens. **JUAN FERNÁNDEZ ISLANDS. Isla Masatierra:** in fruticetis apricis collium, *Bertero 12473* (CONC); Quebrada Pangal, *Marticorena et al. 9172* (CONC, M, OS); Valley Anson, *Meyer 9580* (MO, RSA, UC); San Juan Bautista to Pangal, *Pacheco & Valdebenito 6291* (B, CONC); Valle Colonial, *Sparre 7* (CONC, S); colony, *Skottsberg & Skottsberg 183* (GB, S, UPS); between Pangal and La Centinela, *Stuessy & Crawford 6306* (CONC, OS); between hosteria and San Juan Bautista, *Stuessy & Crawford 6310* (CONC); path to Quebrada Pangal, *Stuessy et al. 6200* (CONC, OS).

CHILE. Prov. Cachapoal: Rancagua, *Frödin 494* (UPS); Termas de Cauquenes, 3 Nov 1952, *Pfister s.n.* (CONC). **Prov. Colchagua:** Las Penas, *Barrientos 1605* (CONC); Cerro Echaurrina, *Montero 736*

(CONC). **Prov. Curicó:** Lipimavida, *Spooner & Contreras 4332* (CONC, F, WIS). **Prov. Talca:** Constitución, Feb 1895, *Philippi s.n.* (SGO); Talca, 13 Oct 1897, *Philippi s.n.* (SGO); Constitución, Nov 1891, *Reiche s.n.* (SGO). **Prov. Linares:** Río Achibuena, *Gereau & Taylor 5171* (ASU, F); Termas de Catillo, *Montero 6276* (CONC). **Prov. Ñuble:** a Quirihue despues de Trehuaco, *Schlegal 756* (CONC). **Prov. Concepción:** Parque Hualpen, *Carrasco 333* (CONC); Concepción, *DeVore 1278* (OSH, UC); Concepción, *Elliot 144* (BM, NY); Punta Hualpén, *Hutchinson 248* (F, GH, UC); 1 km E of Coronel, *Lammers et al. 6316* (C, CONC, F, MEXU, MU, NY); 20 km S of San Pedro, *Lammers et al. 6323* (B, CONC, F, MU); Playa El Soldado, *Lammers et al. 6329* (C, CONC, F, GB, MEXU, MU, NY); 10 km W of Florida, *Lammers et al. 6460* (B, CONC, F, MU); Concepción, *Landrum 8388* (F); San Vicente, *Pennell 12867* (GH, NY, PH, SGO); Talcahuano, Dec 1861, *Philippi s.n.* (SGO); Talcahuano, *Skottsberg & Skottsberg 1377* (GB, S); San Pedro, *Stuessy et al. 6681* (OS). **Prov. Arauco:** Contulmo, *Gunckel 40765* (CONC); 3 km E of Contulmo, *Lammers & Baeza 6510* (CONC, F, MU); Laraquete, 20 Dec 1949, *Ricardi s.n.* (CONC, OS); 4.7 km N of bridge over Lébu, *Spooner 4483* (F, WIS). **Prov. Malleco:** Purén, *Lammers & Baeza 6508* (CONC, F, MU); 9 km W of Purén, *Lammers & Baeza 6509* (F, MU); Nahuelbuto, *Rahn & Ødum 4735* (C); Contulmo, Jan 1902, *Reiche s.n.* (SGO); entre Purén y Contulmo, *Sparre & Smith 156* (CONC, OS). **Prov. Cautín:** Puerto Saavedra, *Aravena 30* (CONC); Trovolhue, *Montero 7904* (CONC); Carahue, *Sparre 3381* (SGO). **Prov. Valdivia:** Niebla, *Bricker 227* (ASU); Valdivia, *Bridges 661* (BM, E, RSA); 20 mi. NE of Valdivia, *Eyerdam 10687* (F, NY, SGO, UC, WTU); Niebla, *Garaventa 5533* (CONC); Huiecolla, *Gardner & Knees 4158* (E, K); Valdivia, *Gunckel 21* (CONC); 1 km W of hwy on road to Corral, *Lammers & Baeza 6463* (CONC, F, MU); 38 km E of Corral, *Lammers & Baeza 6464* (F, MU); 31 km E of Corral, *Lammers & Baeza 6466* (F, MU); 7 km N of Chaihuin Bajo, *Lammers & Baeza 6478* (CONC, F, MU); 10 km E of Mehuin, *Lammers & Baeza 6496* (F, MU); Mehuin, *Lammers & Baeza 6503* (B, F, MU); 6 km S of San Jose de la Mariquina, *Lammers & Baeza 6506* (F, MU); Corral, *Rudolph 6097* (VALD); Angachilla, Dec 1960, *Santos & Retamal s.n.* (ISC); Niebla, *Schmitz 91* (VALD). **Prov. Osorno:** Alencapi, *Rudolph 6091* (VALD); Tres Esteros, *Rudolph 6092* (VALD), *6094* (VALD), *6095* (VALD); La Barra del Río Bueno, *Sparre 4558* (S, SGO). **Prov. Chiloé:** Ancud, *Pennell 12493* (F, GH, NY, PH), 25 Dec 1951, *Pfister & Ricardi s.n.* (CONC).

CULTIVATION. U.S.A. California: Berkeley, *Bracelin 1450* (GB). **GERMANY:** Hamburg, 1834, *anonymous s.n.* (S).

4. Lobelia bridgesii Hook. & Arn., J. Bot. (Hooker) 1:278. 1834. *Rapuntium bridgesii* (Hook. & Arn.) C. Presl, Prodr. Monogr. Lobel. 28. 1836. *Tupa bridgesii* (Hook. & Arn.) A. DC. in DC., Prodr. 7:394. 1839. *Dortmanna bridgesii* (Hook. & Arn.) Kuntze, Revis. Gen. Pl. 972. 1891. TYPE: CHILE. Valdivia, near El Castello de Amargos, *Bridges 663* (HOLOTYPE: K!; ISOTYPES: BM! E! K[2]! NY! RSA! W! [photographs: A! F! MICH!]).

Tupa blanda D. Don in Sweet, Brit. Fl. Gard. (ser. 2) 4:pl. 308. 1835. *Rapuntium blandum* (D. Don) C. Presl, Prodr. Monogr. Lobel. 27. 1836. *Lobelia blanda* (D. Don) Endl., Cat. Hort. Acad. Vindobon. 1:437. 1842. *Dortmanna blanda* (D. Don) Kuntze, Revis. Gen. Pl. 972. 1891. TYPE: GREAT BRITAIN. Kent, Sundridge Park, raised from Chilean seeds by Mr. Malleson (LECTOTYPE here designated: D. Don 1835, pl. 308!). As no original material was located, the plate published with the protologue is here designated as the lectotype.

Rapuntium lucaeanum C. Presl, Prodr. Monogr. Lobel. 27. 1836. *Lobelia lucaeana* (C. Presl) A. DC. in DC., Prodr. 7:383. 1839. *Dortmanna lucaeana* (C. Presl) Kuntze, Revis. Gen. Pl. 972. 1891. TYPE: GERMANY. Cultum in horto botanico berolinensi, semina ex America meridionali orta diguntur, Sep 1835, *anonymous s.n.* (HOLOTYPE: PR!).

Robust perennials, 0.5–2.5 m tall; stems several from the base, normally unbranched, hollow, herbaceous or suffruticose, glabrous; latex white. Lamina 9–24 cm long, 1.8–4.5 cm wide, lanceolate, glabrous; margin minutely serrulate; apex long acuminate, aristate or cirrhose; base sagittate, the pair of basal lobes decurrent on the stem for 12–32 mm.

Inflorescence a 15–55-flowered raceme; bracts lanceolate, 15–60 mm long, the base sagittate, the pair of basal lobes decurrent on the stem for 6–22 mm; pedicels 14–30 mm long, ebracteolate, glabrous or sparsely pubescent with stiff spreading hairs. Hypanthium 4–8 mm long, 6–10 mm in diameter, hemispheric or obconic, glabrous. Calyx lobes 5–10 mm long, 2–4 mm wide, narrowly triangular, glabrous; apex narrowly acuminate, aristate. Corolla 25–36 mm long, pink, glabrous; tube 13–19 mm long, 2.5–4.5 mm in diameter at middle, suberect; lobes 12–16 mm long, 1.5–2.5 mm wide. Filament tube 14–17 mm long; anther tube 6–7 mm long, 2–3 mm in diameter, gray, the dorsal three sometimes with scattered long spreading hairs, and/or all five pubescent with short appressed hairs. Capsule 16–17 mm long, 13–14 mm in diameter, ovoid to subglobose. Seeds 0.5 mm long, 0.4 mm in diameter, broadly ellipsoid, golden tan, minutely foveolate-reticulate. Chromosome number $n = 21$ (Lammers & Hensold 1992; Lammers 1993a).

Icones.—D. Don (1835) [as *T. blanda*]; Hooker (1839); Lemaire (1843) [as *T. blanda*]; Loudon (1844), pl. 66, fig. 2; Lammers (1993b).

Distribution, Habitat, and Phenology.—Endemic to the immediate vicinity of Bahia San Juan in Prov. Valdivia (latitude 39°49'S), in the evergreen temperate rain forest region (cf. Walter 1973) of south-central Chile, at elevations from near sea level up to 200 m. Not infrequent there, on grassy slopes, roadsides, and forest margins, sometimes in company with *L. tupa*. It is most easily found along the road that runs from the main highway south of Valdivia to the little coastal village of Corral. Also collected once (from introduced plants?) in Prov. Cautín and in Prov. Osorno or Llanquihue. Flowering mid-December through early March.

Discussion.—Wimmer (1953) distinguished *L. blanda* (including *L. lucaeana*) from *L. bridgesii* on the basis of subtle differences in the size and shape of the leaves. Study of natural populations convinced me that this variation was of no taxonomic significance. This species is unique in the section (and perhaps in the subgenus) for its pink corolla (cf. Lammers 1993b).

Representative specimens. **CHILE. Prov. Cautín:** Conguillio, *Delgado s.n.* (VALD). **Prov. Valdivia:** Corral, *Brooke 6985* (BM); 24 km SE of Corral, *Gardner & Newton 17* (E); Corral, *Gay 1469* (SGO); Amargos, *Gunkel 29* (BM, F); Corral, *Gunckel & Junge 618* (BH, CONC); La Aguada, *Gunckel 5018* (NY); Castillo San Luis a San Martin, *Klempar s.n.* (VALD); San Carlos, 1987, *Krause s.n.* (CONC, SGO); 31 km E of Corral, *Lammers & Baeza 6465* (B, CONC, F, MU); 4 km E of Corral, *Lammers & Baeza 6470* (CONC, F, GB, MEXU, MU); 2.5 km S of Corral, *Lammers & Baeza 6485* (CONC, F, MU, NY); 36 km E of Corral, *Lammers et al. 7856* (CONC, F, UC); Amargos, *Montero 1341* (CONC); Corral, Mar 1878, *Philippi s.n.* (SGO); Amargos, *Sparre & Smith 397* (CONC, OS, Universidad de Talca); Corral, *Werdermann 1938a* (B, M, S); hills above Corral, *West 4880* (GH, MO, UC). **Prov. Osorno** or **Llanquihue**: Monte Sobre, Lago Llanquihue, 1939, *Santa Cruz s.n.* (BH).

CULTIVATION. GERMANY: Münich bot. gard., 9 Apr 1863, *Kummer s.n.* (M), 30 Aug 1867, *Kummer s.n.* (M), 5 Jul 1869, *Kummer s.n.* (M).

PUTATIVE HYBRID

Lobelia excelsa Bonpl. × **L. polyphylla** Hook. & Arn. *Tupa kingii* Phil., Anales Univ. Santiago 90:189. 1895, 'kingi.' TYPE: CHILE. Valparaíso, Poppe's [Poeppig's] Hill, Dec 1868, *King s.n.* (holotype: SGO-057170! [photograph: GH!]).

Presumably a shrub; stems woody, glabrous. Lamina 4.8–11.2 cm long, 1.3–2.4 cm wide, oblong, glabrous; margin minutely serrulate, particularly toward apex; apex acute; base cuneate. Flowers aggregated into a 18-flowered inflorescence; bracts 28–38 mm long, 4–9 mm wide, oblong, minutely pubescent; pedicels 15–18 mm long, ebracteolate, minutely pubescent. Hypanthium 5–6 mm long, 8–10 mm in diameter, hemispheric or broadly campanulate, minutely pubescent. Calyx lobes 5 mm long, 1 mm wide, narrowly triangular, minutely pubescent; apex acuminate. Corolla 40 mm long, apparently dark reddish-purple, minutely pubescent; tube 23 mm long, 2.5 mm in diameter at middle, curved; lobes 17 mm long, 1 mm wide. Filament tube 21 mm long, dark reddish-purple; anther tube 6 mm long, 2 mm in diameter, pale straw-colored, the dorsal three with scattered long white hairs on the surface toward apex. Fruit and seeds not seen. Chromosome number unknown.

Discussion.—Though *Tupa kingii* was treated as a synonym of *L. polyphylla* by Reiche (1905, 1910) and Wimmer (1953), the type appears to represent a hybrid between that species and *L. excelsa*. It resembles *L. excelsa* generally, particularly in the size and shape of the leaves, but differs in its well-demarcated inflorescence (vs. flowers solitary and axillary) of darker flowers on ebracteolate pedicels, features characteristic of *L. polyphylla*. Various quantitative features of the flowers are intermediate in size: pedicels 15–18 mm long (vs. 7–17 mm in *L. polyphylla* and 12–45 mm in *L. excelsa*); hypanthium 8–10 mm in diameter (vs. 4–8 mm in *L. polyphylla* and 8–15 mm in *L. excelsa*); corolla 40 mm long (vs. 15–25 mm in *L. polyphylla* and 38–65 mm in *L. excelsa*), with tube 23 mm long (vs. 7–17 mm in *L. polyphylla* and 25–42 mm in *L. excelsa*) and lobes 17 mm long (vs. 4–12 mm in *L. polyphylla* and 12–33 mm in *L. excelsa*); and filament tube 21 mm long (vs. 9–15 mm in *L. polyphylla* and 29–47 mm in *L. excelsa*), with anther tube 6 mm long (vs. 4–7 mm in *L. polyphylla* and 8–11 mm in *L. excelsa*). As noted above, this specimen is the sole evidence I have seen of hybridization between these two sympatric species.

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